A RECLASSIFICATION OF LIBOCEDRUS AND CUPRESSACEAE

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With two plates

THE GENUS *Libocedrus*, of the Cupressaceae, is well known as having a remarkably disjunct range. As currently interpreted, the species are widely scattered in lands bordering the Pacific Ocean: one in southern Chile, two in New Zealand, two in New Caledonia, three in New Guinea, one in southern China, one in Formosa, and one in Pacific North America. Such a generic range is indeed unique among the conifers, as it covers more or less equal areas in the Northern and Southern Hemispheres. All other genera are confined either to the northern or southern lands or have but occasional outlying species extending beyond the equator.

The northern and southern species were combined together because of the elongate, basically attached scales and the bi-winged seeds with the wings very unequally developed. These characters, as will be noted below, actually differ to a certain extent between the northern and southern species. It is possible that the resemblance is superficial and due to parallel variation. Two authors, Koch (19) and Kurz (20), noted some differences between the northern and southern species and established independently in the same year 1873 two genera, *Heyderia* and *Calocedrus* respectively, for two of the northern species, but their work was soon disregarded by most subsequent authors. In 1926, Pilger (28), noting the discrepancy between the northern and southern species, divided the genus into two subgenera — *Heyderia*, containing the northern species, and *Eulibocedrus*, the southern. However, he did not emphasize the significance of their fundamental differences, which, in my opinion, are of more value than subgeneric differentiation would indicate.

To clarify the taxonomy of the group of species currently included in *Libocedrus*, it will be helpful to trace briefly the bibliographical history of the genus. The first species of this assemblage were discovered in Chile and named in 1824 as *Thuja chilensis* D. Don and *Juniperus uvifera* D. Don (in Lambert, 21). Another was collected in New Zealand and first named *Dacrydium* (*?*) *plumosum* by D. Don in 1828 (In Lambert, 21, ed. 2). In 1842, W. J. Hooker (12) transferred *Dacrydium* (*?*) *plumosum* to the genus *Thuja*, renaming it *Thuja doniana*. In 1843, Hooker (13) described

[1] This study was initiated several years ago at the National Taiwan University, Formosa, China, and was completed in the Department of Botany, Smithsonian Institution, to the authorities of which the author is indebted for their generosity in placing facilities at his disposal. Thanks are due to the curator of the herbarium of the Arnold Arboretum of Harvard University for the loan of certain specimens of *Libocedrus*. To A. C. Smith and C. V. Morton, U. S. National Herbarium, grateful acknowledgment is made for their kindness in reading the manuscript and offering valuable suggestions.

independently a new species from Chile which he called *Thuja chilensis*; this is regarded as the same species as that described previously as *T. chilensis* D. Don, which is based on a different type; the use of the same specific epithet is a coincidence, Hooker being unaware of Don's species. In 1844, Hooker (14) described a *Thuja tetragona* from Chile, which has turned out to be the same species as Don's *Juniperus uvifera*; in this instance, Hooker did know of Don's species, but was not sure of its identity with his own, inasmuch as Don had described the fruit as that of a true *Juniperus*. These three species of the Southern Hemisphere, attributed by Hooker to *Thuja*, which is otherwise a genus exclusively of the Northern Hemisphere, were made the basis of the genus *Libocedrus* by Endlicher in 1847 (5). I am following Pilger (28) and others in choosing *L. doniana* (Hook.) Endlicher, now correctly known as *L. plumosa* (D. Don) Sargent, as the type species. The other species of Chile, *L. tetragona* (Hook.) Endlicher, later known as *L. uvifera* (D. Don) Pilger, which differs from the other species in the 4-ranked, more or less equal leaves, and tetragonous and fastigiate branches, remained in the genus *Libocedrus* until Florin (7) segregated it to form the monotypic genus *Pilgerodendron* in 1930.

In 1853, Torrey (35) described a species from California as *L. decurrens*, the first species from the Northern Hemisphere attributed to the genus *Libocedrus*. This species differed from the southern species in having three instead of two pairs of cone-scales: a smaller outer pair, a much longer fertile middle pair, and an inner sterile pair fused together into a single plate, a structure not found in the southern species. Noting these differences, Koch (19) in 1873 made the Californian species the type of a genus *Heyderia*.

In the same year that Koch proposed the genus *Heyderia*, Kurz (20) described a plant from Yunnan, China, as *Calocedrus macrolepis*, a new genus considered by him to be related to *Libocedrus* and *Thujopsis*, differing from the former in the seed structure. Both *Calocedrus* and *Heyderia* were combined with *Libocedrus* by Bentham and Hooker (1) in 1880, although they noted that these species differ from the southern species of the genus in having the innermost pair of scales sterile and connate. Since that time these northern species have remained in the genus *Libocedrus*.

In 1867, a second species from New Zealand was named by J. D. Hooker as *L. bidwillii* (15). Another species, *L. austro-caledonica* Brongn. & Gris (2), was discovered in New Caledonia, considerably extending the generic range. The range was further extended by discovery of species in New Guinea and Formosa. Three species have been reported to occur in New Guinea, *L. papuana* F. Muell. (25), *L. torricellensis* Schlechter (ex Lauterbach, 23), and *L. arfakensis* Gibbs (11). The Formosan plant identified as *L. macrolepis* since 1902, has been described as a distinct species, *L. formosana* Florin (6). Recently two more species were discovered in New Caledonia, *L. chevalieri* Buchholz (3) and *L. yateensis* Guillaumin (38). The discovery of these different species from widely separated areas in both the Southern and Northern Hemispheres would make this, in its geographical range, a unique genus in the conifers.

A careful study of herbarium material and literature shows that these northern and southern species are different in their cone-structures and other characters. In all the southern species, including those from New Guinea, there are four scales in two pairs of very different sizes. The outer pair is small and sterile, while the inner pair is about two or three times as large and is fertile, each scale bearing one or usually two seeds at the base. In the three northern species, *L. decurrens*, *L. macrolepis*, and *L. formosana*, there are three pairs of cone-scales. The first pair is small, sterile, and recurved at tip when mature. The second pair is very long, over three to six times the length of the outer pair and fertile, each scale bearing two seeds at the base. The third pair is as long as the second pair or slightly longer and is sterile, the scales being connate throughout their entire length into a flat thin plate.

Of more significance is the fact that the disposition of these cone-scales in the northern and southern species is different. The southern species have their four cone-scales meeting at the edges, or in other words, these are valvately disposed. In this respect they differ fundamentally from *Thuja* and other related genera of the north. In the three northern species of *Libocedrus*, the three pairs of scales are imbricately disposed, the outer pair overlapping the inner. This disposition is exactly the same as in *Thuja*, which also has the innermost pair of cone-scales connate into one piece. In *Thuja* and the northern species of *Libocedrus*, the innermost pair is about the same size as the middle fertile pair. But as it is partly covered by the latter, the exposed parts are narrow and it thus appears to be smaller. Actually it is often slightly longer.

This difference in the disposition of the cone-scales indicates in my opinion that the affinities of the southern species of *Libocedrus* are, among the existing genera of the conifers, not with *Thuja*, but with *Diselma*, *Widdringtonia*, *Fitzroya*, and other related genera of the Southern Hemisphere. In all these genera, the cone-scales meet at their edges and are not imbricate. On the other hand, the three northern species are undoubtedly very close to *Thuja*. The cone of these species approaches closely that of *Thuja*, which, as noted above, has a similarly fused pair of scales in the center but with numerous outer sterile scales. Reduction in the number of these outer cone-scales would result in nearly the exact condition that we have in the cones of the northern species of *Libocedrus*. With a broader generic concept, these species could be included in *Thuja*, and this was the view actually expressed by Voss in 1908 (36). However, the leaves of these species are in apparent whorls of four instead of being strictly decussate as in *Thuja*. This difference in the organization of leaves on the stem as well as the fewer number of scales and unequally developed seed-wings keep these species out of *Thuja*.

The northern species of *Libocedrus* also differ from the southern species in having the scales mucronulate on the back of the tip, in having the seeds less unequally 2-winged, both wings being well-developed but with one about twice as long as the other, and in the generally larger number of stamens. In the southern species, the scales are provided with a short or

long, more or less sharp spine or a bract at the back toward the tip or base or center, and the seed has a long, well-developed wing on one side and merely a narrow membranaceous margin on the other.

In vegetative structures, the northern and southern species of *Libocedrus* are also strikingly different. In the southern species, the leaves are very unequal and strictly decussate, alternately long and very short, the dorso-ventral being very small, and the lateral much larger, keeled and contiguous toward base. The lateral leaves only very slightly overlap the next above, and scarcely overlap laterally the dorso-ventral leaves. In the northern species, the leaves are more strongly decurrent, in apparent whorls of four, and the pairs are of about equal length, the dorso-ventral being narrow, and the laterals keeled, overlapping the next above at their bases and also the dorso-ventral ones laterally, while they themselves are not contiguous below. The leaves are more clearly imbricate in arrangement, reflecting the arrangement of the pistillate cone-scales.

In view of the important differences of the three northern species from the southern species of *Libocedrus* in both vegetative and reproductive characters, it seems desirable to consider the two groups as generically distinct. There are two generic names, *Heyderia* Koch and *Calocedrus* Kurz, published in the same year, available for the northern species. *Calocedrus* appeared in July, 1873; the exact date of publication of *Heyderia* is not known. As *Heyderia* was chosen by Pilger for the subgenus he proposed for the group, it is here adopted in preference to *Calocedrus*, at least until an earlier date for the latter can be definitely established.

The three species from New Guinea differ from the other southern species in certain important characters in both the staminate and ovulate cones. There are four scales in the ovulate cone and these are valvate, as in the other southern species. However, these scales are only slightly woody when mature and bear a large, triangular or ovate appendage on the back near the base or below the center. In the other species usually a short or long spine, or sometimes a triangular bract, is borne either toward the tip or above the center. In the New Guinean species, these appendages are thickened and they assume a slightly shield-like appearance. According to Gibbs (11), in her description of *L. arfakensis*, as the cone increases in size, a swelling appears between the two fertile scales. This swelling gradually develops into two ovate-oblong projections which displace the apices of the scales. The outer scales are modified in the same manner but to a lesser extent. However, as to the outer scales, it appears that they are formed by two bracts coalescing together, the outer becoming the smaller ovate appendage and the inner the scale proper. In *L. torricellensis*, Schlechter (ex Lauterbach, 23) actually described these appendages as bracts attached to the scales; they are found nearly at the base of the outer scales.

The seed-scale complex in the Cupressaceae is shown to develop by the intimate fusion of an axillary seed-scale complex, the sterile part of the flower, which faces the cone-axis and bears ovules in its basal regions, and a bract (10). Together they form the "ovuliferous scale." In the

mature cone, the anterior side of the former is generally suppressed and fused to the bract, and the apophysis of the latter becomes the spine or bract-like appendage on the back of the ovuliferous scale. In the New Guinean species, this fusion is apparently less complete and the inner sterile part of the flower more developed than the bract. As a result the bract appears to be very distinct and of relatively larger size as compared with other Cupressaceae. A case somewhat similar to these species is found in *Libocedrus bidwillii* Hook. f. of Tasmania, which has an ovulate cone more or less approaching these species than other species of *Libocedrus*.

In the staminate flowers, the New Guinean species are very distinct in having numerous scales, spirally arranged instead of decussate. The cells are also more variable in number, varying from three to six. The spiral arrangement of the stamens is a unique character. It transcends the Cupressaceae and suggests some relationship with the Taxodiaceae. In vegetative appearance, these species, with their small decussate leaves of very dissimilar alternate pairs, approach most nearly *Chamaecyparis*. On the basis of these distinctive characters in both the staminate and ovulate cones, the New Guinean species are here segregated as a genus distinct from *Libocedrus, sensu stricto*.

In this connection, it is worthy to note that Peirce (27), in his study of the wood anatomy of the Cupressaceae, noted particularly the heterogeneous nature of the genus *Libocedrus, sensu lato*. He studied wood specimens of the following species: *L. bidwillii* (New Zealand), *L. chilensis* (Chile), *L. decurrens* (North America), *L. macrolepis* (China), *L. papuana* (New Guinea), and *L. uvifera* (Chile), the last being the type of *Pilgerodendron*, proposed by Florin (7) as a separate genus. With regard to the latter, Peirce noted that "the woody anatomy has failed to disclose any features that would warrant giving generic status to that species and not to some of the others, for *Libocedrus* is comparatively heterogenous." The wood anatomy of the other cupressaceous genera studied by him is all uniform and homogeneous within the genus. Perhaps an attempt to investigate further the wood anatomy of *Libocedrus sensu lato* and *Pilgerodendron* along the line of the present scheme of classification will bring out different results.

To summarize, the resemblances of the elongated cones in the northern and southern species of *Libocedrus* are superficial only, probably due to parallel variation. Two groups of species differ from each other in cone-structure as well as vegetative characters. Different affinities are indicated and it is therefore desirable to treat these two groups of species as generically distinct. Among the southern species, those from New Guinea differ from the rest in certain important characters of the ovulate as well as staminate cones and are treated as representing a separate genus. In addition to these three genera, there is *Pilgerodendron*, an earlier segregate from *Libocedrus* made by Florin. The classification of the four genera in question is as follows.

Heyderia K. Koch, Dendrol. 2(2): 179. 1873.

Calocedrus Kurz in Jour. Bot. **11:** 196. *t. 133.* July 1873.
Libocedrus sensu Benth. & Hook. Gen. Pl. **3:** 426. 1880, p. p., non Endlicher.
Libocedrus subgen. *Heyderia* Pilger in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **13:** 389. 1926.

TYPE SPECIES: *Heyderia decurrens* (Torr.) Koch.

Trees; branchlets distichous, strongly compressed. Leaves scale-like, closely and distinctly imbricate, decussate, strongly compressed and decurrent, free only at the obtuse and minutely pointed tip, the pairs of about equal length, the dorso-ventral narrow, the lateral keeled, overlapping the dorso-ventral laterally, not joining together themselves. Flowers monoecious, solitary, terminal on different branchlets. Staminate flowers oblong, consisting of 6–16 decussate scales; anthers sessile, of 4 cells pendulous from the subpeltate, broadly ovate, pointed scale. Ovulate flowers oblong, formed of 6 erect woody imbricate persistent scales, the upper and lower pairs sterile, the middle pair only fertile; ovules 2 at the base of each fertile scale, erect. Mature cone oblong, more or less truncate, maturing the first year, the scales 6, in 3 pairs, woody, imbricate, mucronulate at the back near the tip, the lower pair small, ovate, sterile, recurved at tip, the middle pair much larger, 3–6 times as long as the outer or more, oblong, fertile, erect, the upper pair linear, about as long as or slightly longer than the middle pair, sterile, connate together into a flat woody erect plate. Seeds 2 to each fertile scale, erect, compressed, with 2 unequal, lateral, erect, oblong wings, the larger to nearly as long as the scales, the other about half as long; cotyledons 2.

Three species, one in Pacific North America, one in Formosa, and one in Yunnan, Hainan, and northern Burma.

1. **Heyderia decurrens** (Torr.) K. Koch, Dendrol. 2(2): 179. 1873.

Libocedrus decurrens Torrey in Smithson. Contr. Knowl. **6**(1): 7. *t. 3.* 1853.
Thuja craigiana Murray in Rep. Oreg. Exped. **2:** *t. 2.* 1854.
Thuja gigantea sensu Carriere in Rev. Hort. 1854: 224. 1854, non Nuttall.
Thuja decurrens Voss in Mitt. Deutsch. Dendr. Ges. 1907(16): 88. 1908.

North America, Oregon and California to Lower California, scattered among other coniferous trees at 1,000–2,500 meters.

The following forms are known in cultivation:

Heyderia decurrens f. **compacta** (Beissner) comb. nov.

Libocedrus decurrens compacta Hort. ex Beissner, Handb. Nadelh. 30. 1891.

Heyderia decurrens f. **glauca** (Beissner) comb. nov.

Libocedrus decurrens glauca Beissner in Jäger & Beissner, Ziergeh. ed. 2, 472. 1884.

Heyderia decurrens f. **aureo-variegata** (Schwerin) comb. nov.

Libocedrus decurrens aureo-variegata Schwerin in Mitt. Deutsch. Dendr. Ges. 1907(16): 256. 1908.

2. **Heyderia formosana** (Florin) comb. nov.

Libocedrus formosana Florin in Svensk Bot. Tidskr. **24:** 126. *f. 2 & t. 2.* 1930.
Libocedrus macrolepis sensu Forbes & Hemsl. in Jour. Linn. Soc. Bot. **26:** 540. 1902, p. p., non Benth. & Hook.
Libocedrus macrolepis var. *formosana* Kudo in Jour. Soc. Trop. Agr. (Formosa) **3:** 16. 1931.

Formosa, scattered in broad-leaved forests, rarely forming pure forests, in ravines and on mountain slopes at 150–1,900 meters, in the northern and central part of the island.

3. **Heyderia macrolepis** (Kurz) comb. nov.

Calocedrus macrolepis Kurz in Jour. Bot. **11:** 196. *t. 133.* 1873.
Libocedrus macrolepis Benth. & Hook. Gen. Pl. **3:** 426. 1880.
Thuja macrolepis Voss in Mitt. Deutsch. Dendr. Ges. 1907(16): 88. 1908.

A rare tree, at about 1,400–1,600 meters, southwestern Yunnan and along the Burmese border; also in Hainan.

Pilgerodendron Florin in Svensk Bot. Tidskr. **24:** 132. 1930.

Trees or shrubs, evergreens, the branchlets tetragonous. Leaves small, scale-like, ovate, quadrifarious, decussate, of about equal size, imbricate, adnate below, free and more or less spreading above, dorso-ventrally compressed, keeled on the back. Flowers dioecious, solitary, terminal on branchlets. Staminate flowers relatively large, subcylindric, with elongate scariose-margined basal leaves; scales large, decussate, imbricate; anthers of 4–8, usually 6 cells, pendulous from the subpeltate, short-stalked, erect, scales. Ovulate flowers with 4 elongate, decussate basal leaves, ovoid to ellipsoid, formed of 4 decussate persistent scales, slightly fleshy when young and cohering at margins, the outer smaller, sterile; ovules 2 at the base of each fertile scale, erect. Mature cone ovoid, the scales 4, in 2 pairs, separate, valvate, woody, with a long erect-incurved spine on the back near the tip, the lower scales small, oblong-lanceolate, sterile, the upper scales obovate-oblong, fertile, about 3 times as long as the lower, the axis often projected in the center of the cone into a very short ovoid or rarely subcylindric column. Seeds solitary or 2 at the base of each fertile scale, obtusely triangular, very unequally winged laterally, the longer wing erect, elongate, much longer than the seed, the other very short.

One species in southern Chile.

1. **Pilgerodendron uviferum** (D. Don) Florin, loc. cit. 133. 1930.

Juniperus uvifera D. Don in Lamb. Pin. **2:** 17. 1824.
Thuja tetragona Hook. in Lond. Jour. Bot. **3:** 148. *t. 4.* 1844.
Libocedrus tetragona Endlicher, Syn. Conif. 44. 1847.
Libocedrus cupressoides Sargent, Silva N. Amer. **10:** 134. 1896.
Libocedrus uvifera Pilger in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **13:** 389. 1926.

Southern Chile, western slopes of the Andes from Valdivia southward to Terra del Fuego.

Libocedrus Endlicher, Syn. Conif. 42. 1947.

Libocedrus subg. *Eulibocedrus* Pilger in Engler & Prantl, Nat. Pflanzenfam. ed. 2. 13: 389. 1926.

TYPE SPECIES: *Libocedrus doniana* (Hook.) Endlicher = *L. plumosa* (D. Don) Sargent.

Trees or shrubs; branchlets distichous and compressed, sometimes tetragonous when young. Leaves scale-like or short needle-like, imbricate only at the tip, decurrent, decussate or 3-ranked, compressed, very unequal, the dorso-ventral very small, the lateral much larger, keeled and contiguous below. Flowers monoecious, solitary, terminal on different branchlets. Staminate flowers oblong, of 6–10, decussately arranged scales; anthers sessile, of 4 cells pendulous from the peltate or subpeltate scale. Ovulate flowers ovoid, formed of 4 decussate, erect, woody, persistent scales, the outer smaller, sterile; ovules 2 at the base of each fertile scale, erect. Mature cone ovoid, obtuse, maturing the first year, the scales 4, in 2 pairs, valvate, woody, with a short or long spine or small triangular bract-like appendage on the back above the center or near the tip, the lower scales small, ovate, sterile, the upper scales ovate-oblong, fertile, about 2 or 3 times as long as the lower. Seeds solitary or 2 at the base of each fertile scale, compressed, very unequally winged laterally, the lower wing erect, oblong, to nearly as long as the scale, the other narrow, reduced; cotyledons 2.

Five species, widely scattered in regions bordering the Pacific in the Southern Hemisphere, one in southern Chile, two in New Zealand, and two in New Caledonia.

1. **Libocedrus plumosa** (D. Don) Sargent, Silva N. Amer. 10: 134. 1896; Druce in Rep. Bot. Exch. Cl. Brit. Isles 1916: 633. 1917.

Dacrydium (*?*) *plumosum* D. Don in Lamb. Pin. ed. 2. App. 143. 1828.
Thuja doniana Hook. in London Jour. Bot. 1: 571. *t. 18*. 1842.
Libocedrus doniana Endlicher, Syn. Conif. 43. 1847.

New Zealand, northern and southern islands, in forests, rare.

2. **Libocedrus bidwillii** Hook. f. Handb. N. Zeal. Fl. 257. 1867.

New Zealand, northern and southern islands, on mountain slopes to 2,000 meters.

3. **Libocedrus chilensis** (D. Don) Endlicher, Syn. Conif. 44. 1847.

Thuja chilensis D. Don in Lamb. Pin. 2: 19. 1824.
Thuja chilensis Hook. London Jour. Bot. 2: 199. 1843.
Thuja adina Poepp. & Endl. Nov. Gen. et Sp. 3: 17. *t. 220*. 1845.

Southern Chile, on slopes of mountain valleys, at about 950–1,500 meters.

4. **Libocedrus austro-caledonica** Brongn. & Gris. in Bull. Soc. Bot. France 18, 140. 1871.

New Caledonia, eastern slopes of Mt. Humboldt at about 1,000 meters.

5. **Libocedrus chevalieri** Buchholz in Bull. Mus. Hist. Nat. Paris **21**(2): 283. 1949.

New Caledonia, western slopes of Mt. Humboldt, at 1,450–1,550 meters.

6. **Libocedrus yateensis** Guillaumin in Bull. Mus. Hist. Nat. Paris **21**: 45, 1949.

New Caledonia, right bank of Blue River, at about 200 meters.

Papuacedrus Li, gen. nov.

Arbor alta; ramulis oppositis distichis compressis; foliis decussatim oppositis, adpresse quadrifariatim subimbricatis, difformibus, lateralibus longioribus complicato-carinatis subfalcatis acutis vel subacutis, pro parte maxima adnatis, apice solum liberis, facialibus minutis, planis adpressis squamiformibus triangularibus vel basim ramulorum versus oblanceolatis acutis vel acuminatis; strobilis in diversis ramis monoicis; strobilis staminibus in ramulis terminalibus solitariis cylindricis, antheris 16–∞-seriatis spiraliter dispositis, squamiformibus late ovatis subpeltatis breviter stipitatis chartaceis, loculis 2–6 globosis deorsum 2-valvatis; strobilis ovulatis in ramulis brevibus erectis, elongato-ovatis, squamis 4, decussatis, valvatis, 2 exterioribus sterilibus; strobilis ovulatis maturis ovoideis, squamis demum sublignosis, 2 exterioribus sterilibus ovatis vel oblongis ad basim bractea ovata acuta adnata munitis, 2 interioribus ad basim 2-ovulatis, longioribus lanceolatis subacutis vel rotundatis, exterioribus 2- vel 3-plo longioribus, infra medium bractea triangulari patula praeditis; seminibus 4 ellipsoidalibus plus minusve compressis lateraliter alatis, ala altera elongata, altera subobsoleta.

TYPE SPECIES: *Libocedrus papuana* F. Muell.

A genus of three species in New Guinea and Molucca.

1. **Papuacedrus papuana** (F. Muell.) comb. nov.

Libocedrus papuana F. Muell. in Trans. Roy. Soc. Vict. N. S. **1**(1): 32. 1889.
Thuja papuana Voss in Mitt. Deutsch. Dendr. Ges. 1907(16): 88. 1908.

New Guinea, in northern and southern parts at 1,700–3,000 meters, and Molucca, at about 2,000 meters.

2. **Papuacedrus torricellensis** (Schlechter) comb. nov.

Libocedrus torricellensis Schlechter ex Lauterbach in Bot. Jahrb. **50:** 53. *f.* 2. *H-N.* 1913.

New Guinea, Torricelli Mountains, at about 900–1,000 meters.

3. **Papuacedrus arfakensis** (Gibbs) comb. nov.

Libocedrus arfakensis Gibbs, Phytogeogr. & Fl. Arfak Mts. 84. *f.* 6, *a–b*. 1917.

New Guinea, Arfak Mountains, on ridges and in forests, at 2,300–2,600 meters.

CLASSIFICATION OF CUPRESSACEAE

With the above redefinition of the genera *Libocedrus, Papuacedrus, Heyderia,* and *Pilgerodendron,* a problem which follows is their proper classification within the family Cupressaceae. These genera are segregated mainly on the basis of the ovulate cones, and the structure of the ovulate cone has long been considered as important in classification and of great significance in interpreting relationships in the conifers. A general review of the structure and evolution of the ovulate cone in the Cupressaceae is given by Florin (8,10). He considers the cones in some species of *Juniperus* and in *Microbiota,* in which only one fertile axillary complex and one single ovule is developed, as the most strongly reduced.

It is interesting to note that although the northern and southern genera assigned to the Cupressaceae are grouped in separate taxa in most systems of classification of the conifers, *Libocedrus* has had various dispositions. The first important system was proposed by Endlicher in 1847 (5), in the work where *Libocedrus* was first established. In his order Cupressineae, the Actinostrobeae include these southern genera: *Widdringtonia, Frenela, Actinostrobus, Callitris,* and *Libocedrus*; while the Thujopsideae include the northern genera *Biota, Thuja,* and *Thujopsis.* At that time, it should be noted, only three species of *Libocedrus* were known, all from the Southern Hemisphere, and therefore the scope of the genus was clear and definite and its relationship was correctly indicated by the author.

In later years, when the northern species of the genus *Libocedrus* were discovered, practically all authors of later systems, such as Eichler (4), Neger (26), Vierhapper (37), and Saxton (32), included *Libocedrus* with the northern genera, apparently interpreting the genus on the basis of the northern species only.

A radical change was made by Pilger (28), who combined the northern and southern groups of genera, long referred to two different groups by all authors, into one subfamily Thujoideae under the Cupressaceae. His system of classification of the whole family is as follows:

Subfamily I. Thujoideae: *Actinostrobus, Callitris, Tetraclinis, Callitropsis, Widdringtonia, Fitzroya, Diselma, Thujopsis, Thuja, Libocedrus, Fokienia.*
Subfamily II. Cupressoideae: *Cupressus, Chamaecyparis.*
Subfamily III. Juniperoideae: *Arceuthos, Juniperus.*

The latest system, by Janchen in 1950 (17), classifies the Cupressaceae as follows:

Subfamily I. Juniperoideae.
  Tribe Junipereae: *Arceuthos, Juniperus.*
Subfamily II. Cupressoideae.
  Tribe 1. Cupresseae: *Cupressus, Chamaecyparis, Fokienia.*
  Tribe 2. Thujopsideae: *Pilgerodendron, Libocedrus, Microbiota, Biota, Thuja, Thujopsis.*
  Tribe 3. Actinostrobeae: *Diselma, Fitzroya, Widdringtonia, Neocallitropsis, Callitris, Tetraclinis, Actinostrobus.*

Pilger's system, appearing in a standard reference work, is widely known, but, compared with other systems, it is unsatisfactory in that it combines the usually separated and widely different Actinostrobeae and Thujopsideae into one. This arrangement may serve to obviate the problem of placing the questionable *Libocedrus*, but it obscures the different and divergent trends of development of these genera. Also unsatisfactory is Pilger's placing of *Fokienia* in his Thujoideae instead of Cupressoideae, as the cone of *Fokienia* is essentially the same as that of *Chamaecyparis*; the two should undoubtedly be closely associated, as in Janchen's system, where *Cupressus, Chamaecyparis,* and *Fokienia* constitute the tribe Cupresseae.

Saxton (30, 31, 32), working with embryogeny, considered that the Cupressaceae should be divided into at least two subfamilies: the Callitroideae, containing the genera *Actinostrobus, Callitris* and *Widdringtonia,* and the Cupressoideae, containing the remaining genera of the family. *Tetraclinis* and *Fitzroya* have affinities with both groups, but they should probably be considered as belonging to the Cupressoideae.

Moseley (24) based his evaluation of characteristics on the reproductive morphology and embryogeny, considered by him as of phylogenetic importance in 12 genera, and proposed an entirely different system for the Cupressaceae. The characters are listed in a chart, mostly presented in pairs, considered by him as either primitive or advanced. His modification of Pilger's system is as follows: (genera starred are considered by him as of doubtful status).

Subfamily Cupressoideae: *Cupressus, Chamaecyparis.*
Subfamily Juniperoideae: *Juniperus, Arceuthos*, Microbiota*.*
Subfamily Thujoideae: *Libocedrus, Biota, Tetraclinis, Fitzroya, Thujopsis, Thuja, Diselma*, Fokienia*.*
Subfamily Callitroideae: *Actinostrobus, Callitris, Widdringtonia, Callitropsis*.*

Considering the number of primitive characteristics, Moseley regards the Cupressoideae as lowest in the family and the Callitroideae as the most highly evolved. In the Thujoideae, *Libocedrus* and *Biota* possess the greatest number of primitive characteristics, while *Thuja* and *Fitzroya* are the most advanced. Callitroideae was originally established by Saxton and upheld by Moseley on the basis of these morphological characters: archegonia lateral in position, the absence of a prosuspensor in the embryo, a proembryo that completely fills the archegonium, the absence or obscurity of an archegonial jacket, and a proembryo which is not in definite tiers.

Moseley's phylogenetic scheme is very different from, and in some cases diametrically opposed to the various systems proposed by taxonomists on the basis of external morphology, especialy that of the cone. *Juniperus,* with fleshy fused cone-scales and wingless seeds, is considered by all others as more advanced than those genera in the Thujoideae, which have dry distinct cone-scales and winged seeds (10). In Moseley's system, the order is reversed. He considers that "the Callitroideae possess outstanding characters [as mentioned above] that distinguish them from the other

groups of the Cupressaceae." However, when he compares *Fitzroya* and *Tetraclinis*, two genera in his Thujoideae, with the Callitroideae, he finds in *Fitzroya*, four, and in *Tetraclinis* three important characteristics in common with the latter group.

It remains to be seen whether characters in embryogeny will be sufficient to explain the phylogenetic trends in the Cupressaceae. At the present judgment on the phylogenetic significance of these characters is still controversial. Thomson (34, Radforth, 29) disagrees with Buchholz's idea, which Moseley follows, in the interpretation of certain fundamental phenomena in embryogeny pertinent to the phylogeny of conifers. In some cases, such as polyembryogeny, Thomson's view of the phylogenetic significance is just the reverse of that of Buchholz.

Using mainly the characters of the cone-scales, a revised system of classification for the Cupressaceae is presented below. Among the genera of the family, there are two main types of cones. In one group, the cone-scales are present in pairs or in whorls of three or four. Generally there are two pairs, and only more rarely two ternate whorls or two quadrate whorls. The scales are always thick and usually woody, and are valvate in arrangement, as the scales come into contact at their edges and do not overlap. All genera with cones of this type occur in the Southern Hemisphere, with the exception of the isolated *Tetraclinis*. These genera may be considered as constituting one subfamily, the Callitroideae (PLATE 1).

In this subfamily, there are three genera with ternate whorls: *Fitzroya, Actinostrobus,* and *Callitris*. In *Fitzroya,* there are three whorls of scales, the innermost being very rudimentary and minute, the middle largest and each scale bearing about two or three 3-winged seeds, and the outermost smaller and sterile. In *Actinostrobus,* there are two whorls surrounding a slightly protruding axis, the outer and inner scales being of about equal size and each bearing two 3-winged seeds. In *Callitris,* there are also two whorls, the inner being the larger, each scale bearing many winged seeds, and the outer ones slightly smaller and bearing fewer seeds. Both *Actinostrobus* and *Callitris* may sometimes possess a residuum of very rudimentary scales in the center of the cone as in *Fitzroya*. All three genera have 3-ranked leaves. These genera, of comparatively more primitive character in having ternate scales, few to many, winged seeds, and sometimes a whorl of rudimentary scales in the center, are clearly of close relationship and are here classified as representing one tribe, the Actinostrobeae. It should be noted that *Fitzroya* was described by the publishing author, Hooker, as having imbricate cone-scales. Pilger (28) described the scales as somewhat imbricate. So far as I can make out from herbarium specimens, the thick, coriaceous scales are valvate as in the other southern genera. For a definite determination it will be necessary to have fresh material.

The other southern genera have 2-, 4-, or 8-ranked leaves, and all have cones consisting of two pairs of scales, except *Octoclinis* and *Neocallitropsis* (*Callitropsis*). The cone of these genera has eight scales in two whorls, with a short axis protruding in the center. Each of the inner scales bears

two, winged seeds. The leaves in these genera are in whorls of four. In *Widdringtonia* there are four scales of equal size, each bearing many, winged seeds. In *Diselma, Papuacedrus, Pilgerodendron*, and *Libocedrus,* there are two pairs of scales. In *Diselma,* the two pairs are of about equal size, one sterile and one fertile, the latter bearing at the base of each scale two or three winged seeds. In *Pilgerodendron, Papuacedrus,* and *Libocedrus* the two pairs of cone scales are of unequal size, the outer much smaller and sterile, and the inner larger and fertile, bearing one or two seeds at the base of each scale. These southern genera represent another tribe, the Libocedreae.

Papuacedrus, as noted above, differs from other genera of the Cupressaceae in the spiral arrangement of the scales in the staminate cone. This character may be of phylogenetic significance, as it indicates relationship with the Taxodiaceae. In this connection mention may be made of two genera of the Taxodiaceae with outstanding characters. *Metasequoia* has decussate scales in the ovulate cones, a character transcending the Taxodiaceae and suggesting relationship with the Cupressaceae (16, 33). *Athrotaxis,* of Tasmania, the only genus of the Taxodiaceae of the Southern Hemisphere, has either spirally or decussately arranged leaves and subspirally arranged staminate scales, characters somewhat intermediate between the Taxodiaceae and Cupressaceae. These genera, together with *Papuacedrus*, offer great possibilities in elucidating the relationships between these two families by further investigation.

A third tribe, the Tetraclineae, contains the more or less isolated genus *Tetraclinis* of northern Africa. It is the only genus of the Northern Hemisphere with valvate cone-scales. There are two pairs of cone scales, of equal size but of slightly different shape. The young scales are somewhat fleshy. The vegetative characters mostly closely approach *Heyderia* and *Thujopsis*. The cotyledons are three to five, instead of usually two as in other genera, and this character suggests *Juniperus*. *Tetraclinis* thus shows characters intermediate between the northern and southern genera, but its basically valvate cone-scales indicate closer relationships with those of the south.

In the northern genera, excepting *Tetraclinis,* the cone-scales show more varied development, but basically the arrangement is imbricate. These genera constitute another subfamily, the Cupressoideae. The scales occur in pairs with the exception of *Juniperus* and *Arceuthos,* where the scales are generally present in threes but sometimes also in twos. In this subfamily three tribes are discernible (PLATE 2).

In the first tribe, Cupresseae, including *Cupressus, Chamaecyparis,* and *Fokienia*, the cones, which are essentially globose, bear three to eight pairs of shield-like scales. Most of these scales except usually the outermost and innermost ones, are fertile, each bearing two to many, winged seeds. In the number of scales and seeds, this group is undoubtedly the most primitive. *Cupressus* has six to twelve scales, the fertile ones bearing many seeds each. *Chamaecyparis* also has six to twelve scales, but the fertile scales bear only three seeds each. *Fokienia* has a larger number of scales, varying from twelve to sixteen, but the fertile ones bear only two seeds

each. Because of the thickness of the cone-scales they do not appear distinctly overlapping at the edges. Pilger (28) considers these scales as valvate. However, the outer scales cover the inner ones at almost the entire length and their disposition, much in the same manner as in *Heyderia*, is clearly imbricate. In *Fokienia*, the seeds are more unequal-winged than in the other two genera. This genus is probably more advanced than the other two and serves as a link with the following tribe, which it also resembles very closely in vegetative characters.

The second tribe, Thujopsideae, is characterized by fewer scales, of flat or concave, generally elongate shape. *Thujopsis* has six to eight thick scales, the innermost and outermost pairs being sterile. The fertile scales bear two winged seeds each. In *Thuja*, there are eight to twelve scales, with the innermost pair sterile and often fused into a plate. The middle pairs bear two winged seeds each at the base of each scale. In *Biota*,[2] sometimes included in *Thuja*, the scales are six in number, thick in texture, with the inner pair fused and sterile and the outer bearing one or two wingless seeds each. This genus probably connects with the following tribe, which has fleshy scales and wingless seeds. From *Thuja*, further reduction in the number of scales and seeds resulted in *Heyderia*, with only three pairs of scales, the inner fused and sterile, the middle fertile, and the outer much smaller and also sterile. The seeds are unequally winged.

The last tribe, Junipereae, consisting of *Arceuthos* and *Juniperus*, sometimes combined into one genus, has fleshy cone-scales, separate at first but fused together at maturity. The scales usually appear in two whorls of three each, but occasionally also in pairs. The seeds are wingless. This is undoubtedly the most highly evolved group of the whole family. Although the fleshy connate scales are distinctive, this tribe is clearly linked with the last tribe, inasmuch as *Biota*, with fleshy scales and wingless seeds, is somewhat intermediate. It is thus better treated as an advanced, specialized tribe of the northern subfamily, with imbricate scales, than as a subfamily by itself.

All genera of the subfamily Callitroideae, with the exception of *Tetraclinis*, are of the Southern Hemisphere; while all genera of the subfamily Cupressoideae are of the Northern Hemisphere. *Tetraclinis* occurs in northern Africa, within the range of the hypothetical Gondwana land as with all the rest of the southern genera. The geographical range shows that the two subfamilies have developed independently for a very long time. This pattern of distribution is in accord with that of other group of conifers, where the genera or higher categories are either of the north or of the south. The extraordinary geographical range that has been accredited to *Libocedrus*, *sensu lato*, was based upon a misconception of significant generic characters.

Fossil records have shown that the coniferous floras of the Northern and Southern Hemispheres have been distinct from each other since very

[2] *Microbiota decussata* Komarov is an uncertain genus and species. Rehder (Man. Cult. Trees Shrubs, ed. 2. 55. 1940) suggests it as probably only a variation of *Biota orientalis* (L.) Endl. retaining the juvenile foliage up to the fruiting stage.

ancient times. In North America, for instance, Mesozoic and Cenozoic fossils all pertain to genera of the present northern type, such as *Cupressus*. *Juniperus*, *Thuja*, *Taxodium*, *Sequoia*, *Abies*, *Larix*, *Picea*, *Pinus*, *Psuedotsuga*, *Tsuga*, *Cephalotaxus*, and form genera related to these modern ones (18, 22).[3] Florin (9), in a detailed analysis of the Tertiary fossil conifers from the southern lands, shows the genera to be the same as those now existing in the Southern Hemisphere, and that none of the genera typical of the Northern Hemisphere mentioned above were present. Florin has convincingly proved that the separation of the northern and southern types has existed since the late Palaeozoic. He also indicates, however, that certain genera of the southern group might have forced their way northward into the region primarily occupied by the northern group and vice versa, which is also reflected by the recent distribution of some genera.

A system of classification for the family Cupressaceae is tabulated below. The synonymy of suprageneric groupings in the Cupressaceae, as well as in other conifers, is very complicated. Practically all the tribes given below have been treated at one time or another as families or subfamilies. In a very ancient group like the conifers, the existing genera, mostly of relic nature, naturally do not show intimate relationships between them, as do many more modern groups. The rather burdensome synonymy reflects the varied opinions expressed by many authors. It is suggested that in the conifers, a broader outlook must be taken in presenting systems of classification in order to show the relationships between the existing genera and to render the systems useful for practical purposes. As the synonyms have been given very fully by Janchen (17) in a recent publication, they are not repeated here.

Family CUPRESSACEAE Neger

I. Subfamily CALLITROIDEAE Saxton in New Phytol. **12:** 253. 1913.

A. Tribe **Actinostrobeae** Endlicher, Syn. Conif. 3. 1847, p. p.

1. *Actinostrobus* Miquel (2 species in western Australia).
2. *Callitris* Ventenat (About 20 species in Australia, Tasmania, and New Caledonia).
3. *Fitzroya* W. J. Hooker (1 species, in southern Chile).

B. Tribe **Libocedreae** Li (Actinostrobeae Endlicher, op. cit., p. p.).

Arbor vel frutex; foliis decussatim oppositis; squamis ovulatis 4 vel 8, 2-seriatis, similibus, aequalibus vel inaequalibus.

1. *Neocallitropsis* Florin (*Callitropsis* Compton) (1 species, New Caledonia).
2. *Octoclinis* F. Mueller (1 species, southwestern Australia).

[3] A few doubtful records of fossil material pertaining to *Callitris* and *Podocarpus* are known from the Tertiary of the Northern Hemisphere. Florin noted (9, p. 73) that "Alleged occurrences of detached *Podocarpus* leaves and foliage-shoots in Tertiary strata of the Northern Hemisphere must as a rule be regarded with considerable suspicion," and (9, p. 83) that "All the Tertiary fossil coniferous remains from Europe and North America supposed to belong to *Callitris* appear to be referable to the northern genus *Tetraclinis*."

3. *Widdringtonia* Endlicher (5 species, South Africa and southeastern Tropical Africa).
4. *Diselma* J. D. Hooker (1 species, Tasmania).
5. *Papuacedrus* Li (3 species, New Guinea, Moluccas).
6. *Pilgerodendron* Florin (1 species, southern Chile).
7. *Libocedrus* Endlicher (5 species, southern Chile, New Zealand, New Caledonia).

C. Tribe **Tetraclineae** Li (Tetraclinaceae Hayata in Bot. Mag. Tokyo **46:** 27. 1932).

1. *Tetraclinis* Masters (1 species, Morocco, Algeria, Tunisia).

II. Subfamily CUPRESSOIDEAE K. Koch

A. Tribe **Cupresseae** Neger

1. *Cupressus* Linnaeus (About 12 species, North America, Asia to eastern Mediterranean).
2. *Chamaecyparis* Spach (About 6 species, North America, Japan, Formosa).
3. *Fokienia* A. Henry and H. H. Thomas (1 species, southeastern China to Tonkin).

B. Tribe **Thujopsideae** Endlicher

1. *Thujopsis* Siebold & Zuccarini (1 species, Japan).
2. *Thuja* Linnaeus (5 species, eastern Asia and North America).
3. *Biota* D. Don (1 species, northeastern Asia).
4. *Heyderia* K. Koch (3 species, Pacific North America, Formosa, Hainan, southwestern China to northern Burma).

C. Tribe **Junipereae** Neger

1. *Arceuthos* Antione & Kotschy (1 species, Europe to western Asia).
2. *Juniperus* Linnaeus (About 60 species, widely distributed in the Northern Hemisphere).

SUMMARY

The genus *Libocedrus* is found to consist of two diverse groups of species with basic differences in the cone structure. The genus should be limited to those species, all of the Southern Hemisphere, with four valvate cone-scales. Three species from New Guinea have ovulate scales bracteate below and spirally-arranged staminate scales, indefinite in number, and are segregated from the other species as a distinct genus *Papuacedrus*. The three northern species, with six, imbricate cone-scales, constitute another genus, *Heyderia*. The arrangement of cone-scales seems to be an important character in the classification of the Cupressaceae. As a result of the reclassification of *Libocedrus*, the family Cupressaceae can be reorganized as consisting of two subfamilies. The subfamily Callitroideae is composed of genera with valvate scales and can be divided into three tribes: Actinostrobeae, with ternate scales, Libocedreae, with paired or quadrate scales, and Tetraclineae, with paired dissimilar scales. The subfamily Cupressoideae is composed of genera with imbricate scales and can be divided into three tribes: Cupresseae, with thick, shield-like scales, Thujopsideae, with flat, more or less concave scales, and Junipereae, with fleshy scales coalescing at maturity. All genera of the Callitroideae, with the exception of the isolated *Tetraclinis*, are of the Southern Hemisphere,

while all genera of the Cupressoideae are of the Northern Hemisphere. This distribution pattern, together with their basic difference in the cone-structure, indicates that the two groups are probably of remote relationship, having been long isolated and having developed independently, like many other groups of conifers.

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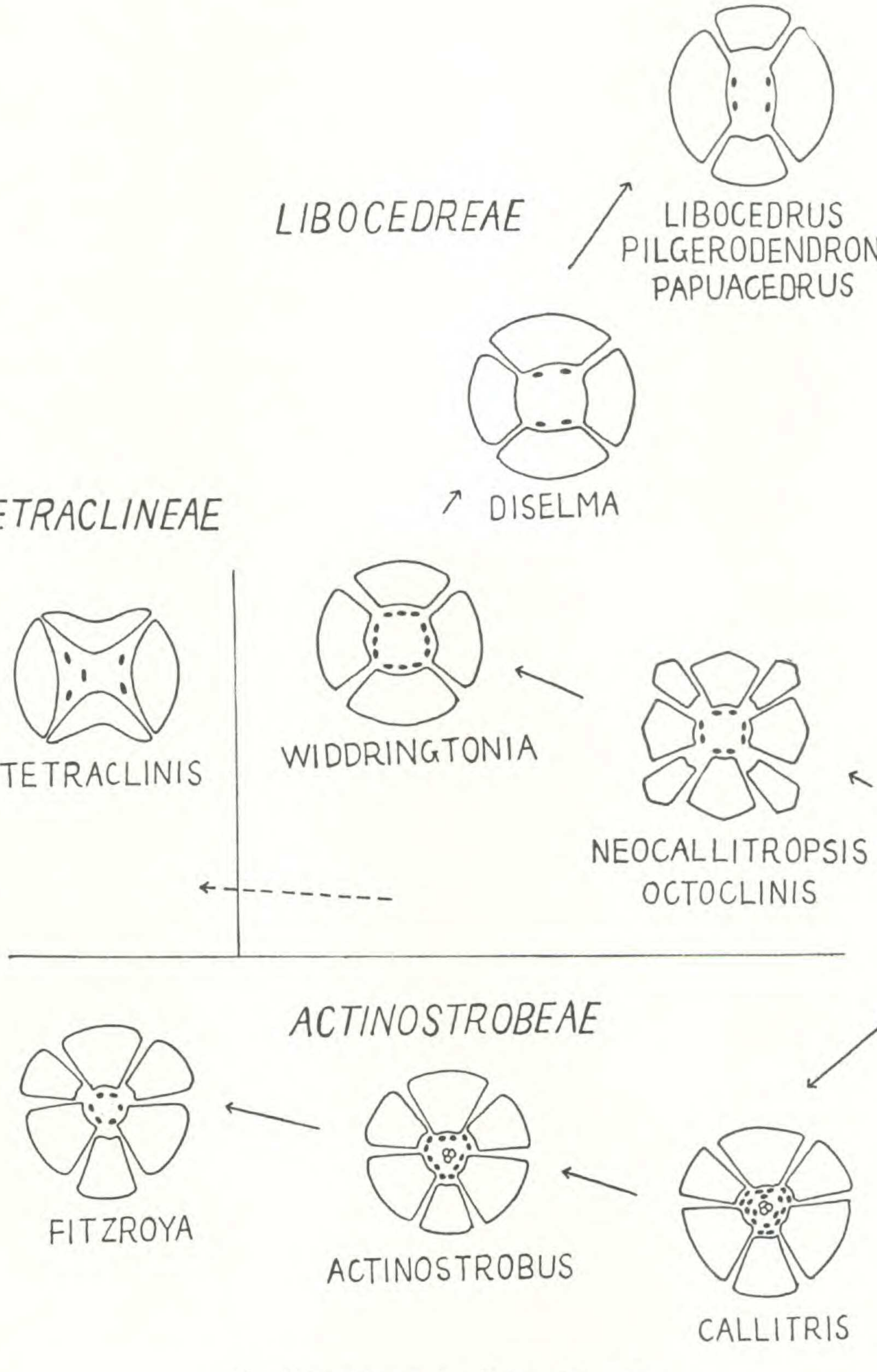
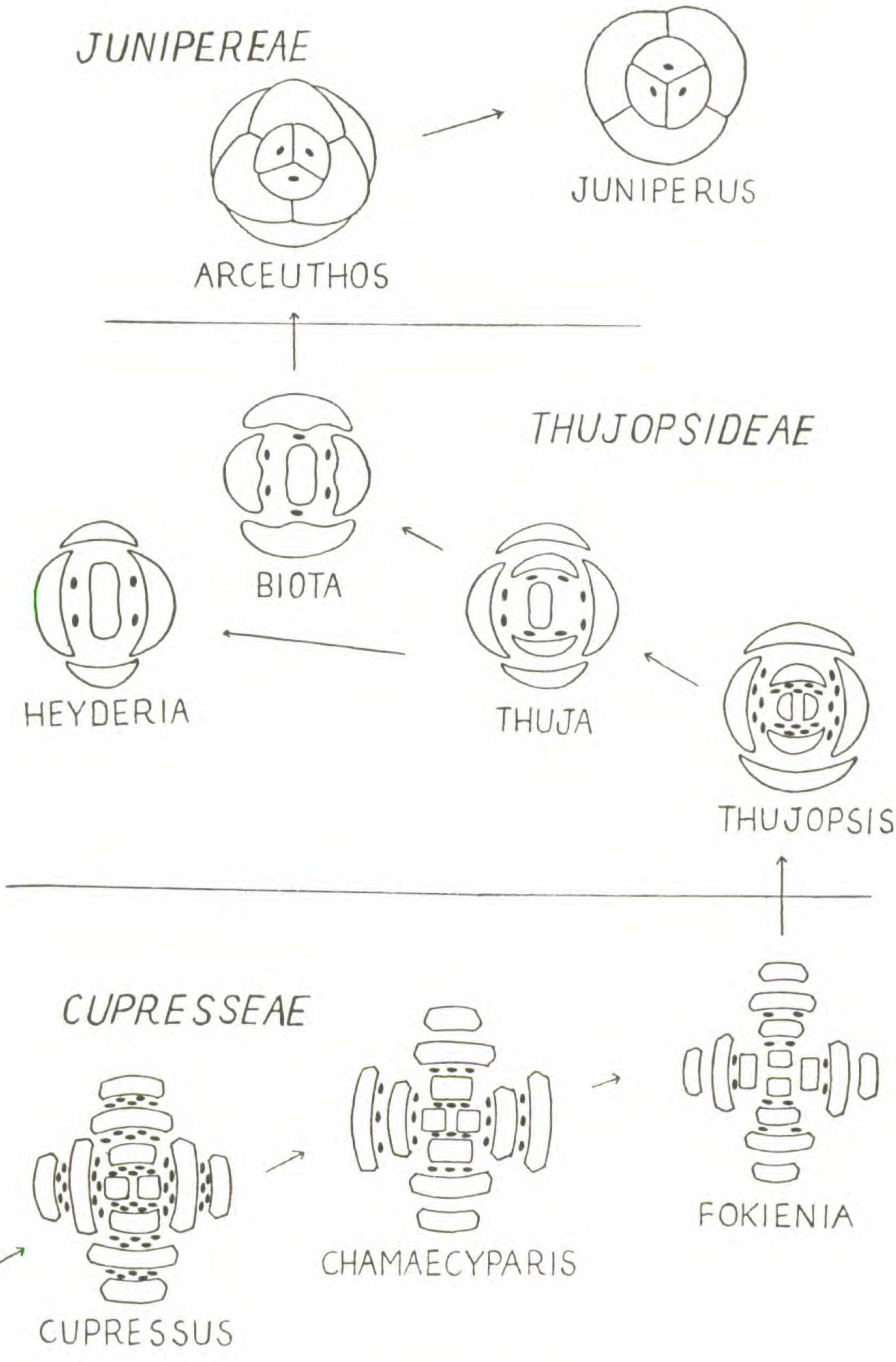
MORRIS ARBORETUM,
PHILADELPHIA, PA.

EXPLANATION OF PLATES

PLATE 1. Diagram showing the hypothetical types of cones of the genera of the subfamily Callitroideae and their probable relationships and directions of evolution.

PLATE 2. Diagram showing the hypothetical types of cones of the genera of the subfamily Cupressoideae and their probable relationships and directions of evolution.


LIBOCEDREAE
LIBOCEDRUS
PILGERODENDRON
PAPUACEDRUS
DISELMA
TETRACLINEAE
TETRACLINIS
WIDDRINGTONIA
NEOCALLITROPSIS
OCTOCLINIS
ACTINOSTROBEAE
FITZROYA
ACTINOSTROBUS
CALLITRIS


JUNIPEREAE
JUNIPERUS
ARCEUTHOS
THUJOPSIDEAE
BIOTA
HEYDERIA
THUJA
THUJOPSIS
CUPRESSEAE
FOKIENIA
CHAMAECYPARIS
CUPRESSUS